III.-On the Pterylography of Photodilus. By W. P. Pycraft, A.L.S., F.Z.S.
(Plate II.)
The following paper gives the result of a carcful study of the pterylosis of an adult specimen of Photodilus badius received recently by the Natural History Museum from Dr. C. Hose, F.Z.S., the Resident at Baram, Borneo.

Observations on this subject have been made before, but no thoroughly detailed account of the pterylosis of Phofodilus has hitherto been given. Although this article claims to be the most nearly complete account of the sulject up to the present time, yet one or two small points still remain to be recorded. These concern the overlap and the relative lengths of the feathers forming the coverts of the dorsal aspect of the wing, which could not well be made out in the specimen to hand.

In the general form and distribution of the pteryle Photodilus is distinctly Asionine in character, but in the form of the external ear it is unique.

I hope, ere long, to have the good fortune to be able to study the pterylosis of Heliodinus. This is now one of the most important forms of the Striges awaiting a detailed description.

## I. Description of the Pleryla.

Pteryla capitis (Pl. II.):-
Fronto-parietal area.-This extends from the base of the beak to the crown of the head, and passing backwards merges into the occipital area. 'Traced from the beak it commences in the form of a broad band bounded on either side by the upper horns of the crescentic loral area. On the crown of the head the band narrows somewhat, widening again before passing into the occipital area, while it is bounded on either side by a well-marked apterium.

Occipital area (Pl. 1I. fig. 3).-This may be said to commence at a point corresponding to the level of the aperture of the left ear as a sudden widening of the fronto-parietal

area. The lateral borders of this tract are semicircular in outline, the tract itself suddenly narrowing at the base of the neck to pass into the pteryla colli dorsalis. The feathers in this area radiate outwards from the middle line on either side.

Loral area (PJ. II. fig. 1). -This is represented by a densely packed crescentic patch of feathers in front of the eye, and is continued forwards on the beak to terminate as a cone-shaped area just below the external narial aperture. This conc-shaped area thus comes to be divided in the middle line from its fellow of the opposite side by the cere, whilst its inferior border runs along the basal portion of the beak, but some distance above the tomium. It then passes backwards behind the gape as a narrow band of feathers to join the circum-aural area.

Ocular area.-This area, as in other Owls , is of great size, orring to the lateral projection of the eyes. The lower lid is clothed by numerous rows of concentrically arranged feathers, which pass upwards at the posterior canthus to form a broad band ruming to the circum-aural area, but first sending forwards a branch to clothe the upper lid. The feathers there differ from those of the lower lid in their greater length. By reason of the feeble development of the vanes they resemble filoplumes; the outermost row performs the function of eyelashes along both eyelids.

Circum-aural area (Pl. II. fig. 1).-This is delimited by a number of closely set stiff feathers forming the periphery of the dise, and corresponding to the feathers of the post-aural folds described by me in Asio accipitrinus (3). It may be traced from the ramal area backwards, upwards, and forwards, till it ultimately fuses with the loral area. Immediately behind the eye it is joined by a broad band from the ocular area. Distinct pre- and post-aural skinfolds are wauting.

Ramal area.-This is partly occupied by the post-aural section of the circum-aural area.

Inter-ramal area.-This is filled by a truncated-conical patch of feathers lying between the symphysis of the mandible and the convergent limbs of the ciremon-amal dise-

Seathers, which may be said to meet below the jaw at this point.

The facial dise is formed by the feathers of the loral and post-aural section of the circum-aural area.

I't. colli dorsalis (text-fig. 3).-This is a densely feathered tract not closely investing the neek, but throughout the greater part of its length supported on a vertical fold of skin. This fold serves to fill up the U-shaped curve formed by the folding of the neck on the body in repose, whilst the feather-tract forms a bridge across the top of the loop. The tract is widest at its confluence with the pteryla capitis, and passes insensibly backwards into the pt. spinatis.

P't. spinalis (text-fig. 3).-It is not possible to draw a hard-

## Text-fig, 3.

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pol ce-ll dors
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Dorsal aspect of Photodilus badius, showing the arrangement of the pteryle.
par: = parapteron.
pt.caud. $=$ pteryla caudalis.
pt.coll.dors. $=$ pteryla colli dorsalis.

$$
\begin{aligned}
& \text { pt.cr }=\text { pteryla cruralis. } \\
& \text { pt.sp }=\quad, \quad \text { spinatis. } \\
& \text { pt.hum. }=" \quad \text { humeralis. }
\end{aligned}
$$

and-fast line between the upper end of this tract and the pt. colli dorsulis. The interscapular and lumbar forks are
both present. The arms of the former are conspicuous, arising at the root of the neek, and terminating on a level with the free end of the scapula. The arms of the latter are fecbly developed, and are represented only by a feeble and ill-defined row of feathers, which, running up to join the interscapular fork, enclose a space.

The stem of the lumbar fork is strong, and extends from the convergence of the pre-acetabular ilia backwards to the uropygimm, in front of which it terminates in a long fork.

Pt. caudde.-'There are twelve rectrices.
P't. colli ventralis (text-fig. 4). -This may be described as a

$$
\text { Text-fig. } 4
$$



Ventral aspect of Photodilus badius, showing the arrangement of the pterylæ.

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pt.corp. = pturya cupitis.
pt.coll.vent. = pteryla colli ven-
    tralis,
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pt.vent. = pteryla ventralis.
pt.cr.= ", cruralis.
tr.= trachea.
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backward continuation of the inter-ramal tract. Near the middle of the neck it forks to accommodate the $\mathbf{U}$-shaped neck, the branches passing, one on either side of the curve, to terminate on the pt. ventralis.

Pt. ventralis (text-figs. $4 \& 5$, pp. 39 \& 41).-This tract in its general features recalls that of the Nyctalinæ. The outer branch of the two rows of feathers is distinct, and runs outward from a little below the summit of the shoulder to the free edge of the patagium. The middle and inner branches divide near the upper third of the furcula, at the point where the inner branch is joined by the pt.colli ventralis. The middle branch is quite distinct, and runs downwards as far as the posterior $\frac{1}{5}$ of the sternum. At a point corresponding with a line drawn across the middle of the sternum this branch gives off the characteristic "hook," which turns abruptly upwards, forwards, and outwards on the hypopteron. The area between the hook and its stem is sparsely covered with semiplumous feathers. The inner, in common with the middle, branch arises at the summit of the shoulder, the two branches beiug given off at the point of contact with the $p t$. colli ventralis: from this point backwards the inner branch runs, first slightly inwards and downwards towards the carina, then slightly upwards till the right and left tracts are divided hy nearly the whole width of the sternal plate; from this point backwards they slowly converge again to terminate in a line with the pubic extremities, but some distance from the cloaca (see text-fig. 4, p. 39).

Pt. femoralis (text-fig. 5, p. 41).-This tract is ill defined and small in extent. The feathers of which it is composed are semiplumous in nature. The femoro-crural band is, however, very distinct, the crural portion terminating some distance below the knee-joint.

Pt. cruralis.-This tract is well defined and invests the whole leg. It is continued downwards over the acrotarsium, and, feebly, in the shape of a few bristles, to the acropodium. The planta is feathered.

Pt. alaris (text-fig. 6, p. 42).
Metacarpo-digitals (primaries) 10 ; 6th longest (reckoning
from within outwards). Vanes neither serrated nor emarginated. The remicle, or reduced llth remex, is entirely

Text-fig. 5.


Lateral aspect of Photodilus burlius, showing the arrangement of the pteryle.
pt.fem. = pteryla femoralis .
$u=$ uropygium. Other letters as before.
wanting. The 8th, 9th, and 10th form a series of progressively shorter feathers, so that the wing has a conspicuously rounded appearance. Sccondaries 13, the
inmermost (13th) searcely distinguishable from its major covert. The wing is diastataxic.

The carpal covert (text-fig. 4, p. 39) is large, and directed forward so that the distal end crosses over the shafts of primaries 1-2.

The carpal remex is much smaller than its covert, but has prescrved its pennaceous character.


Dorsal aspect of left wing of Photodilus badius, to show the contour when extended.

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c . c .=\text { carpal covert. }
$$

3,2,1 show the first three primaries.

$$
1,2,3 \quad, \quad, \quad \text { secondaries. }
$$

## Tectrices:-

T. majores.-The major coverts of the dorsal surface of the manus are small. It is extremely interesting to note that the covert of the 10th remex has taken on the characters of a quill-the remicle-being longer than the coverts proximad. Its pattern of coloration differs from that of the remaining coverts of the row ; but in this particular it resembles its remex, which differs from the other remiges in having the outer web conspicuously barred with black and chestnut on a white ground.

The dorsal major coverts of the secondary remiges are of
uniform length throughout, save only the 6th covert, which is distinctly shorter than the 5 th and 7 th.

The major coverts of the ventral surface are small, and gradually decrease in length from without inwards. The reverse is the case in Asio, to take an example.
T. medice.-On the dorsal surface of the manus this row commences at the 2nd metacarpal remex. On the ventral surface of the manus this row of feathers terminates at the base of the 4 th remex, not the 6 th, as in $A$ sio. On the forearm they are fairly long, and not concealed by the minor coverts.
T. minores.-On the dorsal surface these coverts are wanting on the manus. There appear to be three cubital rows. On the ventral surface of the manus the first row replaces the $t$.medice after the 5 th metacarpal remex. There appear to be but two complete rows. Distad of the 2nd or more preaxial row, the wing-surface is but sparsely clothed by small semiplumous coverts belonging to this series.
T. marginales.-On the dorsal surface there are two rows rumning along the preaxial border of the manus. The greater part of the surface of the patagium is clothed by some four or five rows. The preaxial patagial border is clothed by a closely set band of these feathers which runs inwards to join the pt. humeralis.

On the ventral surface these feathers are small and semiplumous; the postaxial row overlap the $t$. minores, whilst the feathers of the preaxial border are very closely set and directed outwards, to form, with those of the dorsal aspect, a clean patagial edge.

Parapteron.-This is made up of about 8 rows, or rather bundles, of three feathers in each bundle. The distal bundles pass gently into the feathering of the forearm, the proximal into the pt. humeralis.

Hypopteron.-The hypopteron is represented only by a few weak semiplumous feathers, which form but a single row, running along the biceps muscle and merging proximally with the median branch of the $p t$. ventralis.

Ala spuria.-Four strong feathers take part in the formation of the ala spuria.

The distribution of the coverts of the dorsal aspect of the wing agrees with that in other Owls; they form obliquely transverse rows sloping from without inwards instead of being arranged in quincunx.

The rounded form of the expanded wing shews this bird to be a wood-haunting species.

Semiplume, Plume, and Filoplume : -
All these agree in their general distribution with what obtains in Owls generally.

Podotheca.-Clothed with feathers down to the acropodium, which is invested with reticulated scales, among which filoplume-like feathers are scattered.

Claws.-There are no claws on the wing : those of the foot are large, rounded, and curved. The mesial border of the claw of the third digit is produced into a flat, cutting, and slightly serrated edge.

Uropygium napiform, and not tufted.
Apteria :-
Apterium capitis (Pl. II. fig. 3).-The apteria of the head are represented by the bare spaces surrounding the cyelids, the spaces on the sclerotic ring of the eye, and a very broad conspicuous space extending on cither side of the head from the apt. colli laterale, and terminating on the crown of the head above the middle of the eye.

Apt. colli laterale. -Tracel from the base of the neek this may be followed forwards to the symphysis of the lower jaw, and upwards to the region of the middle of the eye.

Apt. trunci laterale, spinale, mesogastrei, crurale, and ale superioris and inferioris do not differ materially from those of Asio, and may be studied in the accompanying figures.

## II. Description of the external Ear.

As will be scen by the figures (Pl. II. figs. 1-3), the aperture of the ear (a.e.) is small, oval in outline, and markedly asymmetrical with regard to the aperture on the opposite side of the head.

On the right side (Pl. II. fig. 2) this aperture lies
immediately above the articulation of the mandible with the quadrate, its long axis pointing obliquely backwards. It leads into a spacious chamber extending upwards and backwards for a considerable distance. The passage to the middle ear lies at the bottom of this chamber.

Immediately above the mouth of the external ear lies a deep fossa (f.). This fossa is entirely open laterally, but is bounded in front by the eye, behind by the post-aural section of the peripheral disc-feathers, above by the base of the post-orbital process, and below by a thin fold of skin, which serves also as the roof of the external aperture of the ear (see PI. II. fig. 2). It appears to correspond to the diverticulum of Asio accipitrinus.

On the left side (PI. II. fig. 1) the aural aperture will be found to occupy a position exactly corresponding to the position of the diverticulum of the right side, whilst the latter is represented by a very shallow trough or groove lying immediately below the aural aperture. The superior angle of the mouth of this aperture will be found to lic on a level with a line drawn backwards and very slightly downwards from the posterior canthus of the eyelid, whilst its long axis is nearly at right angles to the long axis of the skull. The extension upwards and backwards of the aural chamber is much less than in its fellow of the opposite side. The chamber, indecd, on this left side leads almost directly downwards to the tympanum.

If a comparison be made between the apertures of the ears of Photodilus and of Asio, a point of considerable interest and of not a little significance, will at once become apparent. This is that the relation between the diverticulum and the aperture on the two sides of the head is the same in both genera. That is to say, in both genera the diverticulum will be found above the aperture on the right side, below it on the left. This suggests that the fold of skin which divides the diverticulum from the aural aperture on the two sides of the head in Photodilus is the homologne of that more extensive fold performing the same office and ruming from the operculum backwards in Otus.

## III. Summary of Conclusions.

Judged by pterylological characters alone, the position of Photodilus, in the scheme proposed in my earlier paper, seems to be most naturally along with the genera which make up the subfamily Asioninæ, among which it stands as a somewhat aberrant genus with leanings towards Asio. The general conformation of the external ear is quite different from that of any other Owl, but, exterually, it may possibly be regarded as more nearly like that of Asio than that of any other genus. It is, indeed, possible that the external ear of photodilus approximately represents the primitive stage from which the complex external ear of Asio has been derived. The roluminous post-aural fold of the latter may very well have arisen by the development of a fold of skin such as that which supports the peripheral dise-feathers of Photodilus; but it is not easy to see how the operculum cau have arisen. It may be remarked, however, that even in the nearly ripe embryo of Asio there is no suggestion either of the postaural fold or of the operculum.

In Photodilus, as will be seen in Pl. II. figs. 1, 2, there is little or nothing apparent which could give rise to such a fold. It is possible, of course, that the operculum had its origin in a raised fold such as that which forms the anterior boundary of the auditory aperture in Photodilus. If we assume this to be so, then it is possible that the membranous rim bounding the aperture superiorly represents the membranous fold which in Asio runs from the post-aural fold to the operculum and divides the "cavernum" into upper and lower moieties. The transformation in the skull necessary to convert the aural region of a bird like Photodilus into that of Asio is not great, iwasmuch as it could be accomplished by the shifting forwards and reduction of the postorbital process and the vertical extension of the bony "cavernum."

In the general pterylosis of the body, Photodilus perhaps comes nearest to Asio*. It differs therefrom in the

[^0]narrower median branch of the $p t$. ventralis and in the extension upwards to the crown of the head of the apt. trunci laterale. In the latter respect it agrees with Bubo maculosus.

I do not propose to enter further upou the discussion of the question of the systematic position of Photodilus at the present time, as I hope to return to this subject in a future paper, wherein the ostcology and the anatomy of the soft parts will be dealt with, together with a general summary of the literature of the subject. I will only remark that, as Beddard has already conclusively shown, Photodilus is not a near ally of Strix, as has been contended on more than one occasion.

## IV. Revised Key to the Subfamilies and Genera of the Family Asionidæ.

The remarkable character of the external car of Photodilus has rendered necessary a slight revision of the first portion of the "Key to the Families, Subfamilies, and Genera" given in my former paper (3).

The revised portion stands as follows :-


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\(d^{\prime}\). Membranous aperture of ear variable in size, but
        its vertical axis never exceeding the horizontal
        axis of the eyelid; aperture not closed by an
        operculum.
    \(a^{\prime \prime}\). Oil-gland conical ; cere not inflated, but closely
        investing the base of the beak; posterior
        half the height of the anterior division of
        the cavernum
        Bubo.
\(b^{\prime \prime}\). Cere laterally inflated ; anterior and posterior
        divisions of the cavernum of equal height. . Scops.
                                    Ninox.
                                    Sceloglunx.
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V. Titles of the Papers referred to.

1. Beddard, F. E. On Photodilus badius, with Remarks on its Systematic Position. Ibis, ser. 6, vol. ii. p. 239 1890.
2. Nitzsch. Pterylography. English Transl. 1866.
3. Pycraft, W. P. A Contribution towards our Knowledge of the Morphology of the Owls. Trans. Linn. Soc. 2nd ser. Kool. vol. vii. 1898.

## VI. ENPLAN゙ATION OF PLATE II.

Fig. 1. Left side view of the head of an adult Photodilus badius, to shew the form of the external ear. This should be compared with fig. 2the right side of the same head-to shew the asymmetry of the two sides.
a.e. $=$ external aperture of ear.
a.c. $=$ apterium capitis.
E. $=$ eye.
$f$. $=$ fossa-the deep trench bolow the aperture of the ear.
$p . f .=$ the cut bases of the peripheral disc-feathers, seated in a feebly dereloped postaural fold.
pt.coll.vent. = pteryla colli ventralis.
Fig. 2. Right side view of the same head. Letters as before.
Fig. 3. Back view of the same head, to shew the different levels of the right and left external apertures of the ear and the form of the apterium capitis.

$$
\begin{aligned}
r . a . e . & =\text { right aperture of ear. } \\
\text { l.a.e. } & =\text { left } \quad, \quad, \\
\text { pt.coll. } & =\text { pteryla colli dorsalis. } \\
\text { pt.cap. } & =\quad, \quad \text { capitis. }
\end{aligned}
$$


[^0]:    * There is nothing whatever in the pterylosis of this bird which in any way resembles that of Strix. Nitzsch, as Beddard has pointed out, seems to have imagined that a resemblance of the kind existed.

